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A REVIEW OF THE ROUND-EARED BATS OF THE TONATIA SILVICOLA COMPLEX, WITH DESCRIPTIONS OF THREE NEW TAXA

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When Thomas (1910) described *Tonatia laephotis*, he regarded it as the Guianan representative of *T. silvicola* (d'Orbigny), which he distinguished from *T. amblyotis* (Wagner) by its large size and notably by its larger skull. Goodwin (1942), in his review of the entire genus *Tonatia*, regarded *silvicola* as a junior synonym of *amblyotis* and *laephotis* as a separate species. Laurie (1955) accepted Goodwin's conclusion regarding the names *silvicola* and *amblyotis*, but she considered *laephotis* to be another synonym of *amblyotis*. Cabrera (1958) reversed this arrangement and placed *amblyotis* as a junior synonym of *silvicola* because d'Orbigny's name antedates Wagner's *amblyotis* by seven years and thereby has priority; furthermore, he regarded *laephotis* to be a subspecies of *T. silvicola*.

Part of the above described confusion seems to have resulted from general acceptance that two distinct species of large *Tonatia* with an accentuated postorbital constriction occur in the upper Amazon Basin and that their main difference is in size. But no one seems to have ascertained whether the observed size differences are due to sex. To gain some insight into the extent of sexual variation, we compared 10 males with 10 females from the Canal Zone of Panamá, all of which, based on the ossification of the phalanges and the development of a sagittal crest, were judged to be adults. Results of our analyses are presented in Table 1. Of the 14 variates examined, the measurements of males are significantly larger in six; namely, greatest length of skull, zygomatic breadth, length of maxillary

tooththrow, width of rostrum measured across the cingula of the upper canines, mandibular length, and length of mandibular tooththrow (c-m3). *F*-values for the other variates revealed no statistically significant differences.

One cranial feature not included in the statistical analyses is the degree of development of the sagittal crest. Visual observation, however, reveals that this structure is more accentuated in males than in females and that accentuation increases with age. The male judged to be the oldest on the basis of tooth wear has a crest nearly 3 millimeters in height; the youngest, a crest about a third as high. The median height of the crest in the sample of males is about 2 millimeters. In females, height of the crest varies from 0.5 to 1.5 millimeters. Because there are significant differences between males and females in size of the skull, it is essential that they be treated separately in any study involving statistical analyses.

In an effort to determine the identity of Central American specimens, we examined 101 specimens from Guyana (holotype, *Tonatia laephotis* Thomas), Brazil (♀, holotype, *Phyllostoma amblyotis* Wagner), Bolivia (2♀♀), eastern Perú (8♂♂, 15♀♀), western Perú and Ecuador (4♂♂, 13♀♀), eastern Ecuador (5♂♂, 11♀♀), Colombia (1♀), Panamá (14♂♂, 13♀♀), Nicaragua and Honduras (5♂♂, 1♀), México, Guatemala, and Honduras (6♂♂, 1♀). In addition, J. E. Hill provided us with requested measurements of one male and two females in the British Museum of Natural History from Carillo and Coronel, Costa Rica.

For statistical treatment, males and females were separated, and individuals lacking a sagittal crest or with cartilaginous phalangeal epiphyses were omitted from the calculations. The remaining specimens (less the holotypes of *T. laephotis* and *T. amblyotis*) were allocated to six groups. Individuals from Bolivia and Amazonian Perú were considered to be typical of the nominate form of *Tonatia silvicola* and used as a standard for comparison for the remaining five groups. Individuals from western Perú and adjacent Ecuador were placed in sample 2; sample 3 was comprised of individuals from Amazonian Ecuador; sample 4 was comprised of 20 specimens from the Canal Zone of Panamá; sample 5 consisted of nine individuals from Costa Rica, Nicaragua, and Honduras that are large and easily segregated by visual inspection; sample 6 consisted of seven individuals from southern México, Guatemala, and northern Honduras, which are so small when compared with those in sample 5 that the striking differences prompted this study.

TABLE 1. — Selected measurements in millimeters of adult *Tonatia silvicola* from the Panama Canal Zone presented to show the extent of individual and sexual variation in this geographically restricted population. An asterisk indicates a probability of less than 0.05.

Variate	Males (N = 10)				Females (N = 10)				F-value
	Mean	SD	Extremes	CV	Mean	SD	Extremes	CV	
Greatest length of skull	27.99	0.60	27.0-29.2	2.16	27.04	0.74	25.9-28.5	2.75	9.84*
Zygomatic breadth	13.80	0.35	13.3-14.6	2.51	13.11	0.38	12.5-13.8	2.86	18.24*
Cranial breadth	10.76	0.21	10.5-11.0	1.97	10.61	0.24	10.3-11.0	2.24	2.22
Postorbital constriction	4.25	0.12	4.1- 4.5	2.77	4.18	0.17	4.0- 4.6	4.04	1.16
Length maxillary toothrow	9.83	0.21	9.5-10.2	2.15	9.53	0.28	9.1-10.0	2.93	7.35*
Width across upper molars	8.85	0.11	9.0- 9.7	1.22	8.67	0.38	8.0- 9.1	4.35	2.10
Width across upper canines	6.08	0.15	5.9- 6.4	2.43	5.75	0.23	5.4- 6.0	4.04	14.39*
Mandibular length	17.67	0.33	17.2-18.2	1.85	16.93	0.45	16.1-17.6	2.64	17.84*
Mandibular toothrow c-m3	10.94	0.23	10.6-11.2	2.08	10.55	0.25	10.2-11.0	2.42	13.05*
Length of forearm	52.06	1.62	49.0-54.8	3.11	52.01	2.30	49.5-56.8	4.41	0.003
Length of foot	15.70	0.48	15.0-16.5	3.08	15.67	0.72	15.0-17.5	4.61	0.01
Length of calcar	16.63	0.91	15.0-17.8	5.50	16.60	0.87	15.0-18.0	5.28	0.005
Length of tibia	23.59	1.14	22.0-25.0	4.83	23.46	1.32	22.0-26.0	5.62	0.05
Length of ear from notch	33.60	1.07	32.0-35.0	3.20	33.80	1.14	32.0-35.0	3.36	0.16

TABLE 2. — Comparative measurements of the six samples of male *Tonatia* covered in this report. Mean, extremes, and plus-or-minus one standard deviation are given for each variate.

Sample area	Greatest length of skull	Zygomatic breadth	Cranial breadth	Maxillary toothrow	Breadth across upper third molars	Breadth across upper canines	Mandibular length	Mandibular toothrow	Forearm
Eastern Perú N = 8	27.84	13.60	10.76	9.71	8.86	6.14	17.55	10.74	55.05
	26.6-28.4 0.77	13.0-14.0 0.41	10.5-11.0 0.18	9.3-10.0 0.27	8.7-9.2 0.16	5.8-6.4 0.20	16.6-18.1 0.51	10.5-11.0 0.34	53.5-56.5 1.22
Western Perú N = 4	28.02	13.25	10.55	9.78	8.85	6.05	17.65	10.95	55.03
	27.8-28.7 0.45	13.0-13.5 0.24	10.5-10.7 0.10	9.5-9.9 0.19	8.5-9.0 0.24	6.0-6.1 0.06	17.5-18.0 0.24	10.8-11.2 0.19	54.0-55.5 0.71
Eastern Ecuador N = 3	28.90	13.43	10.73	9.86	8.73	6.27	18.10	11.07	54.06
	28.8-29.0 0.10	13.1-13.9 0.42	10.6-10.9 0.15	9.8-9.9 0.06	8.7-8.8 0.06	6.0-6.4 0.23	17.9-18.2 0.17	10.9-11.2 0.15	54.0-54.2 0.12
Panama Canal Zone N = 10	27.99	13.80	10.76	9.83	8.85	6.08	17.67	10.94	52.06
	27.0-29.2 0.60	13.3-14.6 0.35	10.5-11.0 0.21	9.5-10.2 0.21	8.7-9.0 0.11	5.9-6.4 0.15	17.2-18.2 0.33	10.6-11.2 0.23	49.0-54.8 1.62
Honduras-Costa Rica N = 6	29.33	13.78	10.95	10.03	9.05	6.46	18.12	11.06	54.97
	28.8-30.2 0.51	13.4-14.2 0.30	10.8-11.0 0.08	9.9-10.4 0.19	8.9-9.3 0.16	6.3-6.6 0.13	17.8-18.4 0.22	10.8-11.6 0.27	51.5-56.4 1.77
México-Honduras N = 6	25.83	12.33	10.06	8.85	7.97	5.55	16.03	9.72	49.94
	24.8-26.9 0.81	12.2-12.7 0.20	9.9-10.2 0.10	8.5-9.0 0.20	7.8-8.2 0.14	5.4-5.6 0.15	15.2-16.5 0.48	9.5-10.0 0.20	47.2-52.7 1.99

TABLE 3. — Comparative measurements of the six samples of female *Tonatia* covered in this report. Mean, extremes, and plus-or-minus one standard deviation are given for each variate.

Sample area	Greatest length of skull	Zygomatic breadth	Cranial breadth	Maxillary toothrow	Breadth across upper third molars	Breadth across upper canines	Mandibular length	Mandibular toothrow	Forearm
Eastern Perú and Bolivia N = 15	27.04	12.91	10.35	9.51	8.75	5.72	17.02	10.59	53.38
	25.7-28.3 0.75	12.4-13.5 0.29	10.0-10.6 0.18	8.9-10.0 0.33	8.2-9.1 0.22	5.1-6.0 0.25	16.0-17.9 0.50	9.9-11.0 0.33	50.0-56.2 1.76
Western Perú N = 12	26.59	12.58	10.29	9.43	8.56	5.43	16.80	10.98	53.75
	25.9-27.2 0.43	12.0-12.8 0.23	10.0-10.5 0.19	9.2-9.6 0.12	8.3-8.8 0.16	5.2-5.6 0.15	16.3-17.1 0.26	10.0-10.7 0.20	52.3-56.4 1.28
Eastern Ecuador N = 10	27.59	12.83	10.28	9.63	8.65	5.73	17.26	10.77	54.21
	26.8-28.5 0.48	12.4-13.2 0.25	9.6-10.7 0.33	9.3-9.9 0.18	8.3-9.0 0.20	5.5-6.1 0.18	16.5-17.8 0.34	10.4-11.0 0.19	51.5-57.2 1.88
Panama Canal Zone N = 10	27.04	13.11	10.61	9.53	8.67	5.75	16.93	10.55	52.01
	25.9-28.5 0.74	12.5-13.8 0.38	10.3-11.1 0.24	9.1-10.0 0.28	8.0-9.1 0.38	5.4-6.0 0.23	16.1-17.6 0.45	10.2-11.0 0.25	49.5-56.8 2.30
Nicaragua-Costa Rica N = 3	29.17	13.83	10.87	9.93	9.03	6.0°	17.6	11.1	55.6
	28.4-29.7 0.68	13.6-14.1 0.25	10.7-11.0 0.15	9.6-10.2 0.31	9.0-9.1 0.06		17.2-17.8 0.35	10.7-11.4 0.36	54.4-56.5 1.08
México-Honduras N = 1	26.0	12.6	10.4	8.8	7.8	5.2	15.5	9.8	50.0

Results of our univariate analyses are presented in Tables 2 and 3. Based on our analyses, individuals in sample 6 (southern México to northern Honduras) appear to us to be specifically distinct from those in the other five samples. In size, they are closest to *Tonatia carrikeri* (J. A. Allen), another member of the *silvicola* complex, in that they have an accentuated postorbital constriction and a well-developed sagittal crest, and might actually represent a geographic race of that species. The other five samples appear to us to be assignable to three geographically varying subspecies of *Tonatia silvicola*. Individuals from sample areas 1, 3, and 4 (Amazonian Perú, eastern Ecuador, and Panamá) appear to represent the nominate form, *T. s. silvicola*, the type locality of which is in Bolivia between the Securé and Isibara rivers. The population occupying the dry Río Chira basin in western Perú and Ecuador are considerably paler, have smaller middle lower premolars, and represent an unnamed geographic race. Individuals in sample area 5 (Costa Rica, Nicaragua, and northeastern Honduras) are readily separated from all the others by their larger size and brighter dorsal coloration. These, too, appear to be representatives of an unnamed geographic race of *T. silvicola*. In size, they appear to be most like *T. s. laephotis* Thomas from the Guianas and eastern Brazil, representatives of which (excluding the holotype) were not examined because we did not consider them essential to solving the problems at hand. These three new taxa are described below.

Tonatia silvicola occidentalis, new subspecies

Holotype. — Adult female, skin and skull, TCWC 11704, from 4 mi. W Suyo, 1000 ft., department of Piura, Perú; obtained by Dilford C. Carter on 31 July 1964, original no. 5357.

Distribution. — Known only from the drainage basin of the Río Chira in southwestern Ecuador and northwestern Perú.

Diagnosis. — Similar in size to *T. s. silvicola* in the upper Amazon Basin (see Tables 2 and 3), but paler dorsally (grayish brown rather than chocolate brown), more extensively whitish ventrally, and with distinctive whitish postauricular patches; skull and dentition similar to those of the nominate subspecies except that the middle lower premolar of *occidentalis* is about half as large and the lower incisors are smaller. Selected measurements of the holotype are: greatest length of skull, 27.1; zygomatic breadth, 12.6; cranial breadth, 10.4; postorbital constriction, 4.0; maxillary toothrow, 9.5; width across M3-M3, 8.5; breadth of rostrum across cingula of the canines, 5.6;

mandibular length, 17.1; mandibular toothrow (c-m3), 10.4; forearm, 53.5; foot (measured from back of base of calcar), 16; calcar, 17; ear from notch, 34; weight, 21.1 grams.

Specimens examined (18). — ECUADOR: *Loja*: 15 mi. N Catacocha, 2000 ft., 1♂ (TCWC). PERU: *Piura*: 4 mi. W Suyu, 1000 ft., 3 ♀♀ (TCWC), Salitral, 4 ♂♂, 10 ♀♀ (FMNH).

Tonatia silvicola centralis, new subspecies

Holotype.—Adult female, skin, skull and body skeleton, TCWC 18774, from El Castillo, 40 m., department of Río San Juan, Nicaragua; obtained by Dillard C. Carter on 15 May 1967, original no. 7813.

Distribution.—Currently known from the Caribbean versants of Honduras, Nicaragua, and Costa Rica.

Diagnosis.—Similar to the nominate form in the upper Amazon Basin, but larger (see Tables 2 and 3), paler—reddish brown above rather than chocolate brown and pale buff rather than dark buff below—and with pale buff postauricular patches. Selected measurements of the holotype are: greatest length of skull, 28.4; zygomatic breadth, 13.6; cranial breadth, 10.7; maxillary toothrow, 9.6; width across M3-M3, 9.0; breadth of rostrum across cingula of upper canines, 6.0; mandibular length 17.8; mandibular toothrow (c-m3), 10.7; forearm, 56.5; foot (measured from back of base of calcar), 18; calcar, 18.5; ear, 34; weight, 29.4 grams.

Specimens examined (6). — HONDURAS: *Olancho*: 40 km. E Catacamas, 500 m., 3♂♂ (TCWC). NICARAGUA: *Río San Juan*: El Castillo, 40 m., 1♂, 1♀ (TCWC); 1 km. S El Castillo, 130 m., 1♂ (TCWC). In addition, J. E. Hill provided measurements of three individuals from Costa Rica—1♂ from Carillo and 2♀♀ from Coronel (32 and 27 km., respectively, NE San José, province of San José, near headwaters of Río Sucio)—that are assigned to this taxon.

Specimens Examined and Assigned to T. s. silvicola

BRAZIL: *Moto Grosso*, 1♀ (holotype of *Phyllostoma amblyotis* Wagner, ZMB). BOLIVIA: *Sarà*: Río Dolores, 400 m., 1♀ (FMNH); Buena Vista, 450 m., 1♀ (CM). PERU: *Cuzco*: Kiteni, 1500 ft. (66 km. from Rosalina on road from Quillabamba, 1♂, 1♀ (LSU); Marcapata (Heda, Cadena), 2♂♂, 4♀♀ (FMNH). *Huánuco*: Tingo María, 1♀ (FMNH). *Junín*: Chanchamayo, 3♂♂ (FMNH). *Loreto*: Pucallpa, 180 m., 2♀ (FMNH); 61 mi. SE Pucallpa, 500 ft., 1♂, 1♀ (TCWC); Yarinacocha, 160 m., 1♂, 6♀♀ (FMNH). ECUADOR: *Napo Pastaza*: Montalvo, Río Bobonazo, 3♀♀ (FMNH); Río Pinto Yacu, 1♂, 1♀ (FMNH); Río Capihuara (0° 29'S, 77° 14'W), 2♂♂, 1♀ (FMNH); Río Suno below Loreta, 1♀ (FMNH). COLOMBIA: *Tolima*: Espinal, 1♀ (FMNH). PANAMA: *Canal Zone*: Ft. Sherman, 7♂♂, 7♀♀ (UMMZ); Rodman, 3♂♂, 3♀♀ (UMMZ). *Darién*: Cerro Quia, 740 m., 1♂ (KU); Río Tuirá at Río Mon, 130 m., 4♂♂, 2♀♀ (KU).

Tonatia evotis, new species

Holotype. — Adult female, skin and skull, TCWC 17142, from 25 km. SSW Puerto Barrios, 75 m., department of Izabal, Guatemala; obtained by Dilford C. Carter on 2 March 1966, original no. 6576.

Distribution. — Currently known from southeastern México and the Caribbean versants of Guatemala and Honduras.

Diagnosis. — Similar to *T. s. silvicola* from the upper Amazon Basin, but smaller (see Tables 2 and 3) and with weaker dentition; differs from *T. s. centralis* in darker colors both dorsally and ventrally, in lack of light postauricular patches, and in much smaller size. Compared with *T. carrikeri* from Venezuela, *evotis* differs in darker coloration, both above and below, and in larger size. Selected measurements of the holotype of *evotis*, followed by those of two females of *carrikeri* in parentheses, are: greatest length of skull, 26.0 (24.0-25.0); zygomatic breadth, 12.6 (10.8-11.1); cranial breadth, 10.4 (9.5-9.6); postorbital constriction, 4.1 (3.7-4.1); maxillary toothrow, 8.8 (8.0-8.5); width across M3-M3, 7.8 (7.5-7.6); breadth of rostrum across cingula of molars, 5.2 (4.7-4.7); mandibular length, 15.5 (14.9-15.0); mandibular toothrow (c-m3), 9.8 (9.0-9.5); forearm, 50.0 (45.5-47.4); foot, 15 (14-14.9); calcar, 14.6 (14-15); weight, 19.8 grams (not available for *carrikeri*). The difference in relative size between *T. evotis* and *T. s. centralis* is illustrated in Figs. 1 and 2.

Remarks. — We were unable to examine the specimen from Free-town, Belice, in the Carnegie Museum listed by Goodwin (1942), but its measurements place it with *T. evotis*.

Specimens examined (7). — MEXICO: Veracruz: 4.1 km. S, 3 km. W Tenochtitlán, 22 m., 2♂♂ (UMMZ). Chiapas: 19 km. S Mapastepec, 25 ft., 1♂ (UMMZ). Tabasco: 1 mi. E Teapa, 1♂ (LSU). Campeche: 12 km. W Escárcega, 1♂ (KU). GUATEMALA: Izabal: 25 km. SSW Puerto Barrios, 1♀ (TCWC). HONDURAS: Gracias a Dios: Puerto Lempira, 1♂ (LSU).

On the Spelling of silvicola and laephotis

The species-group name *Tonatia silvicola* derives from *Lophostoma silvicolum* d'Orbigny, 1836, as the name first was spelled on plate 6 of the *Atlas Zoologique* of the *Voyage dans l'Amérique Méridionale*. Later, d'Orbigny and Gervais (1847) published a description of this species under the name *Lophostoma sylviculum*. According to Article 32 of the *International Code of Zoological Nomenclature* adopted by the XV International Congress of Zoology, the stem *silvicol-* is the correct original spelling.

As originally printed, the diphthong *ae* in *laephotis* was set as a ligature in a typeface that caused it to look much like the diphthong *oe*. For that reason, the name sometimes was misspelled *loephotis* (for example, see Goodwin, 1942). Thomas was silent on the etymology of the specific epithet but he certainly must have taken it from the Greek *λαιός* (properly Latinised as *laeus* and meaning left-handed, awkward, or clumsy — Laius, the father of Oedipus, was left-handed and had an awkward or clumsy gait) plus *φῶσ* (Latinised as *phos* and meaning light, as in sunlight). In combination, the two words *λαιός φῶσ* would indicate clumsy movement or flight in daylight.

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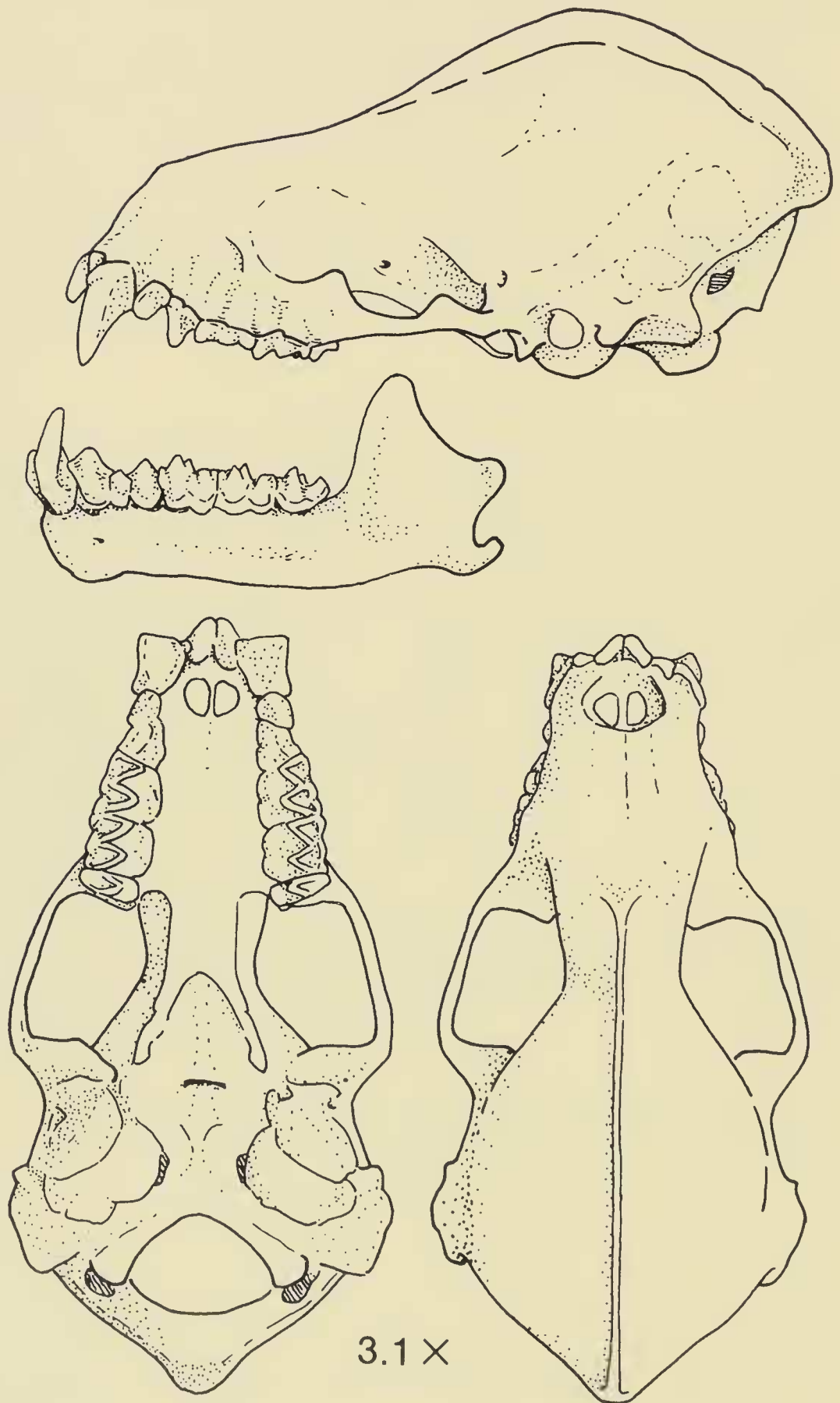


FIG. 1.—*Tonatia silvicola centralis*. Holotype, TCWC 18774 ♀.

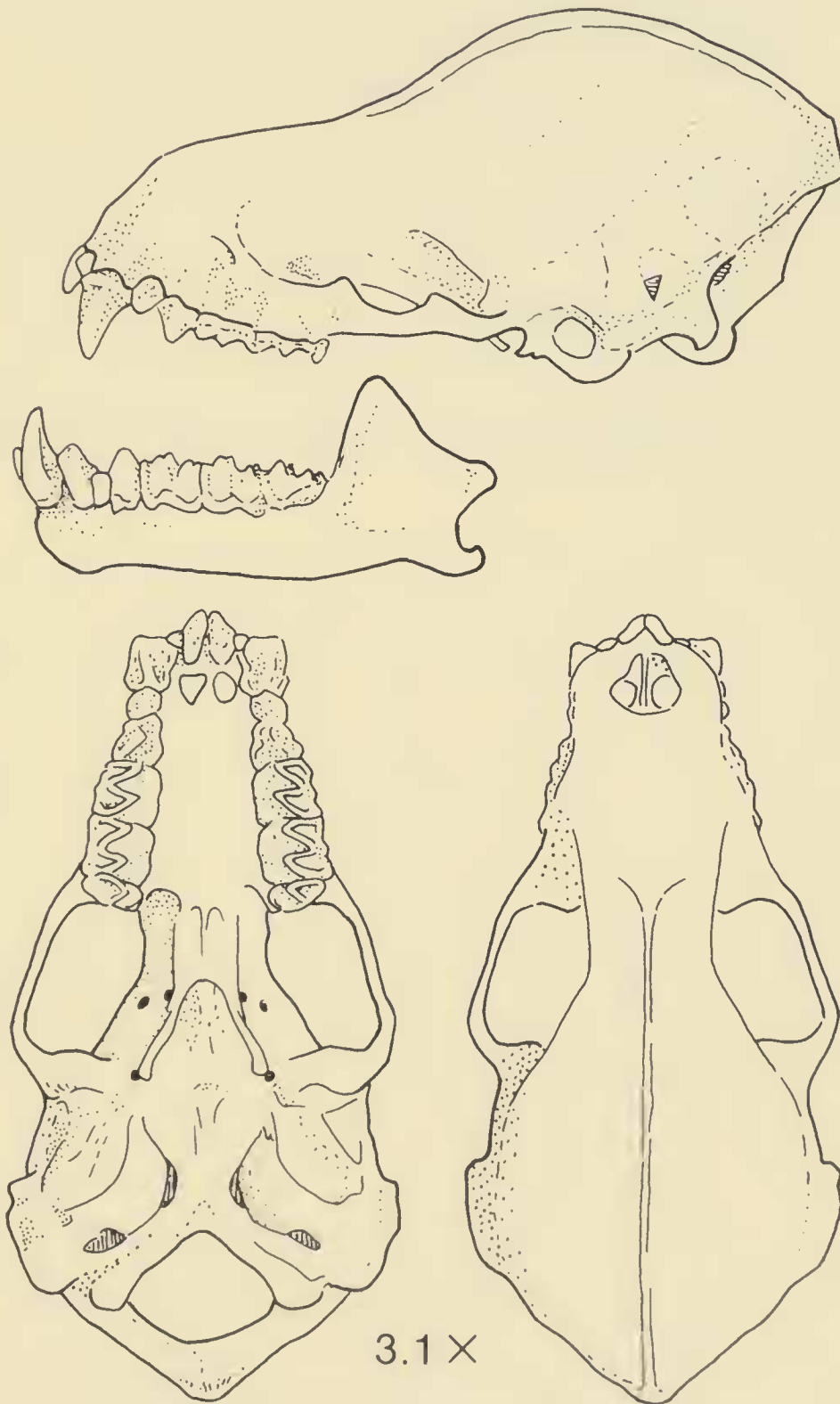


FIG. 2.—*Tonatia evotis*. Holotype, TCWC 17142 ♀.

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